CHAPTER 4:
ENVIRONMENTAL CHARACTERISTICS

RESULTS

Physical Characteristics

Abiotic Environment

Five variables described abiotic environmental characteristics of reaches: elevation, precipitation, distance from stream mouth, aspect, and basin orientation. The sample reaches ranged in elevation from 1887 to 2690 m ($\bar{x}$ = 2106.0, SE = 19.17), and average precipitation ranged from 50 to 203 cm ($\bar{x}$ = 92.2, SE = 3.87) (Table 21). East and west aspects (34% each) were most prevalent, followed by south (24%) and north (9%). Reaches were relatively evenly distributed among the basin orientations: north side = 20, east side = 20, south side = 16, and west side = 24.

TABLE 21. Continuous variables describing the abiotic environment and channel characteristics at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Minimum	Maximum	Average	SE
Abiotic environment:				
Elevation (m)	1887	2690	2106.0	19.17
Precipitation (cm)	50	203	92.2	3.87
Channel characteristics:				
Gradient (%)	0	24	7.1	0.58
Width (m)	0.9	19.0	5.0	0.46
Sinuosity	1.01	2.60	1.20	0.02

Channel Characteristics

Channels were characterized by 4 variables: width, sinuosity, gradient, and channel type. Channel width ranged widely from 0.9 to 19.0 m ($\bar{x}$ = 5.0, SE = 0.46), and was highly correlated (r = 0.972, P < 0.001) with channel area, which ranged from 183 to 4899 m^2 ($\bar{x}$ = 1497.8, SE = 133.66) (Table 21). Sinuosity also ranged widely from 1.01 to 2.6 ($\bar{x}$ = 1.2, SE = 0.02) (Table 21). Gradient ranged widely within and among reaches, with reach averages ranging from 0 to 24% ($\bar{x}$ = 7.1, SE = 0.58) (Table 21).

Gradients of Physical Characteristics

Six variables were entered into the principal components analysis to identify gradients of physical characteristics in the basin: channel gradient, elevation, precipitation, channel width, distance from the mouth, and sinuosity. Correlations among variables were relatively low (r = 0.087 to 0.607), with 9 correlations with $P \leq 0.10$ (Table 22).

TABLE 22. Significant correlations ($P \leq 0.10$) among measures of abiotic and channel environmental variables. Bolded values indicate $P \leq 0.05$. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Variable 1	Variable 2	r	*P*
Elevation	Distance to mouth	**0.607**	**<0.001**
Precipitation	Elevation	**0.292**	**0.009**
Precipitation	Channel sinuosity	0.205	0.068
Precipitation	Channel width	**0.556**	**<0.001**
Precipitation	Distance to mouth	**0.429**	**<0.001**
Channel gradient	Elevation	**0.365**	**0.001**
Channel gradient	Channel width	**-0.326**	**0.003**
Channel gradient	Channel sinuosity	**-0.430**	**<0.001**
Channel sinuosity	Channel width	**0.226**	**0.044**

The analysis resulted in 2 factors with eigen values of > 1.0 for a total of 66.1% of the variation explained among reaches (Table 23). Factor 1 accounted for 34.4% of the variation and represented an elevational gradient, as described by positive associations with elevation, precipitation, and distance from the stream mouth. Factor 2 accounted for 31.7% of the variation and was associated with large, low-gradient, sinuous streams (narrow-fast to wide-slow channel flow).

Vegetation Characteristics

Vegetation Community Composition

The number of vegetation classes occurring at any one reach ranged from 1 to 6 classes (Table 24). The frequency of occurrence of vegetation classes ranged from 6 to 77 reaches. The maximum percent cover ranged from 66.0% (shrub) to 100 % (mixed conifer). Mean coverage ranged from a low of 4.4% (shrub) to a high of 35.4 % (mixed conifer).

TABLE 23. Principal components analysis of channel and abiotic environmental variables. Bolded values indicate variables most associated with the factor. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Variable	Factor 1 scores	Factor 2 scores
Distance from mouth	**0.847**	0.046
Elevation	**0.801**	-0.407
Precipitation	**0.704**	0.473
Channel width	0.293	**0.728**
Channel sinuosity	-0.008	**0.685**
Channel gradient	0.229	**-0.761**
Eigen value	*2.06*	*1.90*
Variation explained (%)	*34.40*	*31.70*

TABLE 24. Frequency and abundance of vegetation classes across sample reaches (n = 80) in the Lake Tahoe basin.

Vegetation variable	Frequency (%)	Minimum	Maximum	Average	SE
Mixed conifer	56.3	0	100.0	35.4	4.20
Lodgepole pine	31.3	0	93.5	9.0	2.25
Subalpine conifer	30.0	0	90.1	17.3	3.35
Aspen–cottonwood	16.3	0	46.7	2.4	0.89
Alder–willow	96.3	0	72.2	19.5	1.45
Shrub	26.3	0	66.0	4.4	1.22
Meadow	47.5	0	93.3	10.5	2.25
Canopy cover index	-	1	94.5	52.0	2.92
Small snags	68	0	286.7	46.7	6.02
Large snags	81	0	56.7	15.0	1.54
Small logs	95	0	1995.3	374.0	41.62
Large logs	88	0	678.9	148.8	16.7
Channel log volume	86	0	9270.3	562.3	155.16

Correlation coefficients among vegetation classes ranged from r = 0.011 to 0.590, with 7 significant correlations (Table 25). Mixed conifer and lodgepole pine were the most strongly related to other vegetation classes. Mixed conifer and lodgepole pine were negatively correlated with subalpine conifer, and with eachother. Meadow had opposing relationships with mixed conifer (negative) and lodgepole pine (positive). Lodgepole pine was present on 25 reaches, and co-occurred with meadow on 19 reaches (76% of the time). Alder–willow was uniquely negatively correlated with mixed conifer, and shrubs were uniquely negatively correlated with lodgepole pine. In addition, canopy cover index was correlated with 3 vegetation classes, being negatively correlated with meadow (r = -0.390, P < 0.001) and lodgepole pine (r = -0.402, P < 0.001), and positively correlated with mixed conifer (r = 0.470, P < 0.001).

TABLE 25. Significant correlations ($P \leq 0.10$) among the abundance values for vegetation classes. Bolded values indicate $P \leq 0.05$. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Variable 1	Variable 2	r	P
Mixed conifer	Subalpine conifer	**-0.590**	**<0.001**
Mixed conifer	Alder–willow	**-0.263**	**0.018**
Mixed conifer	Meadow	**-0.400**	**<0.001**
Lodgepole pine	Mixed conifer	**-0.432**	**<0.001**
Lodgepole pine	Meadow	**0.224**	**0.046**
Lodgepole pine	Subalpine conifer	-0.203	0.070
Lodgepole pine	Shrub	-0.188	0.095

A principal components analysis conducted on the 7 vegetation classes resulted in 4 factors with eigen values > 1.0, explaining a total of 78% of the variation among reaches (Table 26). Factor 1 explained 26.5% of the variation and represented the gradient in lower elevation forest types (below the subalpine zone) of mixed conifer to lodgepole pine with meadow. Factor 2 explained 20.8% of the variation and represented an elevational gradient of mixed conifer and lodgepole pine to subalpine conifer and shrubs. Factor 3 explained 16.4% of the variation and represented alder–willow abundance. Factor 4 explained 14.4% of the variation and represented aspen–cottonwood abundance.

TABLE 26. Vegetation community principal components analysis for sample reaches (n = 80) in the Lake Tahoe basin. Variables were log-normal transformed. Bolded values indicate variables most associated with the factor.

Variable	Factor 1 scores	Factor 2 scores	Factor 3 scores	Factor 4 scores
Meadow	**0.799**	-0.033	-0.295	0.295
Lodgepole pine	**0.656**	-0.479	0.298	-0.269
Mixed conifer	**-0.771**	-0.484	-0.319	0.197
Subalpine conifer	0.100	**0.772**	0.028	-0.443
Shrub	-0.031	**0.602**	0.013	0.161
Alder–willow	-0.004	0.014	**0.950**	0.063
Aspen–cottonwood	0.034	0.028	0.046	**0.868**
Eigen value	*1.85*	*1.45*	*1.14*	*1.01*
Variation explained	*26.5%*	*20.8*	*16.4%*	*14.4%*

Vegetation Structure

Canopy cover and woody debris variables were used to describe vegetation structure (Table 24). The canopy cover index, ranged widely among reaches (range = 1-95%, $\bar{x}$ = 52.0, SE = 2.92), and had a relatively uniform variance across reaches (0-20%, n = 13; 21-40%, n = 13; 41-60%, n = 19; 61-80%, n = 22; 81-100%, n = 13). Snags occurred on 89% (n = 71) of the reaches and logs occurred on 95% (n = 76) of the reaches (Table 24). Small diameter snags (10 to 50 cm dbh) ranged in density from 0 to 286.6 snags/ha ($\bar{x}$ = 46.67/ha, SE = 6.022). Large diameter snags (> 50 cm dbh) ranged in abundance from 0 to 57/ha ($\bar{x}$ = 15.0/ha, SE = 1.54). Small logs (25 to 50 cm diameter) ranged in abundance from 0 to 1995.3 m/ha ($\bar{x}$ = 374.0/ha, SE = 41.62), and large logs (> 50 cm diameter) ranged in abundance from 0-678.9 ($\bar{x}$ = 148.8, SE = 16.7). Channel logs occurred in 99% (n=79) of the reaches (Table 24). Total volume of all channel logs per reach ranged from 0 to 9270.3 m^3/ha ($\bar{x}$ = 562.3, SE = 155.16). Correlations among snag and log variables ranged from 0.169 to 0.658, with most correlations being significant (Table 27).

TABLE 27. Correlations among woody debris variables. Bolded values indicate $P \leq 0.10$. Shading represents redundant cells. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

	Small logs		Large logs		Small snags		Large snags	
Variable	r	*P*	r	*P*	r	*P*	r	*P*
Small logs								
Large logs	**0.658**	**<0.001**						
Small snags	**0.451**	**<0.001**	**0.293**	**0.008**				
Large snags	**0.443**	**<0.001**	**0.650**	**<0.001**	**0.506**	**<0.001**		
Channel log volume	**0.362**	**0.001**	**0.321**	**0.004**	**0.236**	**0.035**	0.169	0.134

A PCA was conducted on 5 woody debris variables: small and large log densities, small and large snag densities, and channel log volume. The PCA produced one factor explaining 53.8% of the variation in woody debris among reaches (Table 28). All 5 variables loaded on this factor, with logs having the highest factor scores.

Relationships Between Physical and Vegetation Gradients

Variation in vegetation community composition, abundance, and structure often reflects major environmental gradients. I compared the factor scores of the 2 physical environment gradients, 4 vegetation gradients, and the 1 woody debris gradient to explore relationships between physical and biotic environmental gradients.

TABLE 28. Principal components analysis of snag and log densities on sample reaches (n = 80) in the Lake Tahoe basin. Variables were log-normal transformed.

Variable	Factor 1 score
Large logs	0.834
Small logs	0.819
Large snags	0.787
Small snags	0.669
Channel log volume	0.506
Eigen value	*2.69*
Variation explained	*53.8%*

Each biotic gradient was regressed on each physical gradient (Table 29). The subalpine vegetation gradient and the snag and log gradient were positively related to the elevation–precipitation gradient. The aspen–cottonwood gradient was negatively related to the elevation–precipitation gradient. The forest to meadow gradient was positively related, and subalpine vegetation gradient was negatively related, to the channel flow gradient. The snag and log gradient was positively related to the elevation–precipitation gradient. These regression relationships imply that the distribution and abundance of vegetation characteristics are strongly influenced by physical environmental gradients.

TABLE 29. Linear regression relationships between biotic and physical environmental gradients (derived by principal components analysis) at reaches (n = 80) in the Lake Tahoe basin sampled 1995 to 1996. Beta = partial regression coefficient.

Environmental gradient	B	SE of B	Beta	T	P
Elevation–precipitation gradient by:					
Forest to meadow gradient	0.136	0.112	0.136	1.208	0.231
Subalpine vegetation gradient	0.405	0.104	0.405	3.917	<0.001
Alder–willow gradient	0.076	0.113	0.076	0.671	0.504
Aspen–cottonwood gradient	-0.431	0.102	-0.431	-4.214	<0.001
Snag and log gradient	0.213	0.111	0.213	1.928	0.058
Channel flow gradient by:					
Forest to meadow gradient	0.449	0.101	0.449	4.434	<0.001
Subalpine vegetation gradient	-0.188	0.111	-0.188	-1.687	0.096
Alder–willow gradient	0.094	0.113	0.094	0.838	0.405
Aspen–cottonwood gradient	-0.180	0.111	-0.180	-1.620	0.109
Snag and log gradient	-0.176	0.111	-0.176	-1.584	0.117

In addition to comparisons of physical and biotic gradients, I explored regressions between the snag and log gradient and vegetation gradients (Table 30). The snag and log gradient was negatively related to forest to meadow and aspen–cottonwood gradients. No other regressions were significant.

TABLE 30. Linear regression models between the snag and log gradient and 4 vegetation environmental gradients (derived by principal components analysis) at reaches (n = 80) in the Lake Tahoe basin sampled 1995 to 1996. Beta = partial regression coefficient.

Vegetation gradient	B	SE of B	Beta	T	P
Forest to meadow	-0.460	0.101	-0.460	-4.580	<0.001
Subalpine vegetation	0.008	0.113	0.009	0.075	0.940
Alder–willow	0.098	0.113	0.098	0.871	0.387
Aspen–cottonwood	-0.200	0.111	-0.200	-1.803	0.075

Environmental Characteristics by Basin Orientation

Abiotic Environment

Precipitation showed patterns of variation by orientation (P < 0.001), whereas elevation did not vary (ANOVA, P = 0.119) (Table 31). West side reaches had the highest precipitation and east side reaches had the lowest precipitation (Table 32).

Channel Characteristics

All 3 channel characteristics varied significantly by basin orientation (Table 31). Channel gradient was highest on north side reaches and lowest on south side reaches (Table 32). Channel width was greatest on south side reaches and least on east side reaches (Table 32). Finally, sinuosity was highest on south side reaches and lowest on north and east side reaches (Table 32).

Vegetation Characteristics

The proportion of reaches occupied by each vegetation class varied significantly by basin orientation for 5 of the 7 vegetation classes: mixed conifer, subalpine conifer, lodgepole pine, aspen–cottonwood, and alder–willow (Table 33). Mixed conifer was most abundant on east side reaches and least abundant on north side reaches (Table 34). Aspen–cottonwood was also most abundant on east side reaches and absent from south side reaches (Table 34). Subalpine conifer had a distribution opposite that of mixed conifer, being most abundant on west side reaches and least abundant on east side reaches (Table 34). Alder–willow was similarly most abundant on west side reaches, but least abundant on south side reaches (Table 34). Finally, lodgepole pine was most abundant on south side reaches and least abundant on east side reaches (Table 34).

TABLE 31. Analysis of variance results for physical variables by basin orientation. SS = sum of squares. ν = degrees of freedom. MS = mean square. Data were collected at sample reaches (*n* = 80) in the Lake Tahoe basin, 1995 to 1996.

Source of variation	ν	SS	MS	F	*P*
Precipitation:					
Between groups	3	4.76	1.58	29.25	<0.001
Within groups	76	4.12	0.05		
Total	79				
Elevation:					
Between groups	3	0.036	0.012	2.018	0.119
Within groups	76	0.457	0.006		
Total	79	0.493			
Channel gradient:					
Between groups	3	6.31	2.10	4.66	0.005
Within groups	76	34.34	0.45		
Total	79				
Channel width:					
Between groups	3	16.78	5.59	38.00	<0.001
Within groups	76	11.19	0.15		
Total	79				
Channel sinuosity:					
Between groups	3	0.07	0.02	4.78	0.004
Within groups	76	0.38	0.01		
Total	79				

TABLE 32. Significant ($P \leq 0.05$) relationships between basin orientation and the 5 abiotic environment and channel variables. Results are based on individual analysis of variance tests. Mean and standard errors of untransformed variables are presented. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Basin orientation: North side (1) $\bar{x}$	SE	East side (2) $\bar{x}$	SE	South side (3) $\bar{x}$	SE	West side (4) $\bar{x}$	SE
Precipitation	79.1	3.33	63.1	2.38	99.3	8.65	122.7	6.94
Channel gradient	9.5	1.29	7.7	1.01	4.6	0.95	6.3	1.08
Channel width	3.4	0.38	1.7	0.15	9.4	1.28	6.3	1.08
Channel sinuosity	1.1	0.02	1.1	0.01	1.3	0.09	1.2	0.03

TABLE 33. Analysis of variance results for vegetation classes by basin orientation. SS = sum of squares. ν = degrees of freedom. MS = mean square. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Source of variation	ν	SS	MS	F	*P*
Mixed conifer:					
Between groups	3	3.127	1.042	4.243	0.008
Within groups	76	18.669	0.246		
Subalpine conifer:					
Between groups	3	2.194	0.731	4.513	0.006
Within groups	76	12.316	0.162		
Lodgepole pine:					
Between groups	3	1.012	0.337	4.031	0.010
Within groups	76	6.360	0.084		
Aspen–cottonwood:					
Between groups	3	0.240	0.080	3.700	0.015
Within groups	76	1.643	0.022		
Alder–willow:					
Between groups	3	0.248	0.083	2.701	0.052
Within groups	76	2.323	0.031		
Shrub:					
Between groups	3	0.189	0.063	1.592	0.198
Within groups	76	3.004	0.040		
Meadow:					
Between groups	3	0.402	0.134	1.462	0.232
Within groups	76	6.966	0.092		

TABLE 34. Significant ($P \leq 0.05$) relationships between basin orientation and the 7 vegetation classes. Results are based on individual analysis of variance tests. Mean and standard errors of untransformed percent coverage are presented. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Vegetation class	Basin orientation							
	North side (1)		East side (2)		South side (3)		West side (4)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Mixed conifer	20.6	7.54	56.1	8.28	25.7	8.47	37.0	7.64
Subalpine conifer	16.4	6.14	0.7	0.68	19.2	8.61	30.8	7.23
Lodgepole pine	5.8	3.83	0.4	0.23	19.3	7.61	12.1	3.99
Aspen–cottonwood	0.4	0.25	6.4	2.54	0	0	2.4	1.94
Alder–willow	20.9	2.66	18.4	3.64	13.5	2.63	23.2	2.30

Woody debris varied by basin orientation, with large logs and small snags varying significantly among orientations (Table 35). For large logs, west side reaches had the highest amount and north side reaches had the lowest amount (Table 36). Small snags were most abundant on east side reaches and least abundant on north side reaches (Table 36).

TABLE 35. Analysis of variance results for woody debris variables by basin orientation. SS = sum of squares. ν = degrees of freedom. MS = mean square. Data were collected at sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Source of variation	ν	SS	MS	F	P
Small logs:					
Between groups	3	17.501	5.834	1.856	0.144
Within groups	76	238.917	3.144		
Large logs:					
Between groups	3	31.895	10.632	2.282	0.086
Within groups	76	354.163	4.660		
Small snags:					
Between groups	3	36.541	12.180	2.600	0.058
Within groups	76	355.992	4.684		
Large snags:					
Between groups	3	2.512	0.837	1.144	0.337
Within groups	76	55.627	0.732		
Channel log volume:					
Between groups	3	0.844	0.281	0.110	0.954
Within groups	76	194.357	2.557		

TABLE 36. Significant ($P \leq 0.05$) relationships between basin orientation and the 5 woody debris variables. Results are based on individual analysis of variance tests. Mean and standard errors of untransformed percent coverage are presented. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin, 1995 to 1996.

Woody debris variable	Basin orientation: North side		East side		South side		West side	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Large log	113.8	22.49	125.1	38.59	142.8	38.78	201.6	31.44
Small snag	20.3	6.74	72.3	17.82	38.8	8.44	52.5	9.06

Canopy cover index also varied among basin orientations (ν = 3, 76; SS = 13,221.304, 40,816.081; MS = 4407.101, 537.054, F = 8.206, $P < 0.001$). Canopy cover index was highest on east side reaches and lowest on south side reaches.

Environmental Conditions by Basin Orientation

The 4 basin orientations were ranked from low (rank = 1) to high (rank = 4) in terms of values for each environmental variable that differed among orientations, and patterns of the ranks were graphed (Fig. 14). For most variables, north and east sides had the two lowest values compared to south and west sides of the basin. Precipitation, channel width, channel sinuosity, subalpine conifer, lodgepole pine, and large logs were all greater on the south and west sides compared to the north and east sides of the basin. In contrast, channel gradient and canopy cover index were all greater on the north and east sides compared to the south and west sides of the basin. Mixed conifer, small snags, aspen–cottonwood, and alder–willow had similar patterns of association with orientation, being highest on the east and west, and lowest on the north and south.

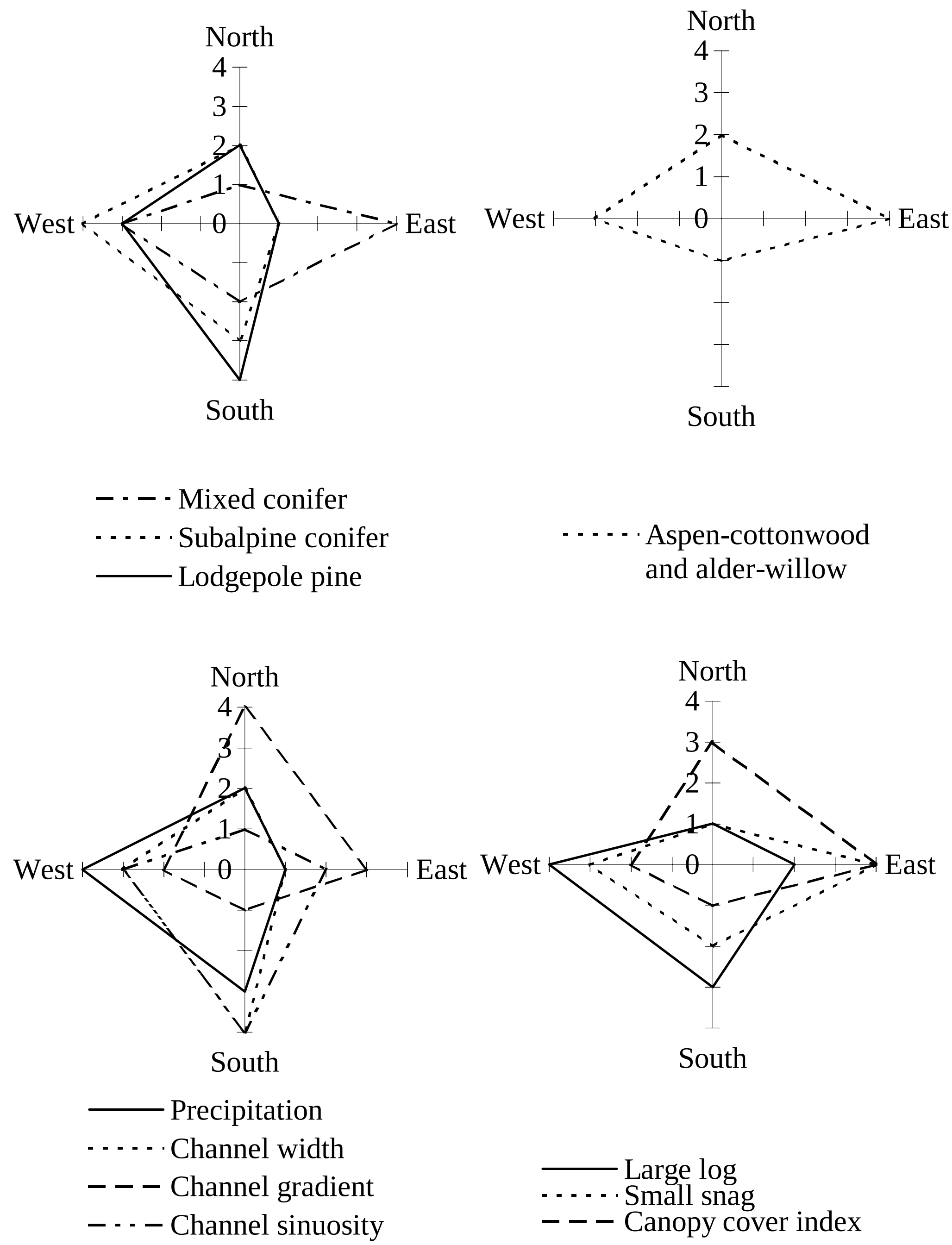

FIG. 14. The average values for 11 environmental variables in rank order by basin orientation. Axes demarcate rank values from 1 (lowest value) to 4 (highest value) across the 4 orientations.

DISCUSSION

Physical Environment

Elevation and Precipitation

For a relatively small area, the basin has 'steep' gradients in abiotic environmental factors, represented in this study by elevation and precipitation. The 800-m elevational range represented by the sample reaches is commensurate with elevational ranges used in other studies of the response of species to elevational gradients (e.g., Terborgh 1971, Able and Noon 1976, Ogden and Powell 1979, Vazquez and Givnish 1998, Young et al. 1998). The 150 cm/yr precipitation range represented by the sample reaches is also substantial and comparable with other studies of precipitation gradients in temperate environments (e.g., Harrington et al. 1995, Dahlgren et al. 1997). Elevation and precipitation were confounded in the study area, and their interrelationship was represented in the first physical PCA factor. Together, elevation and precipitation are known to represent a complex interaction of environmental factors such as decreasing mean temperatures, decreasing growing season length, increasing precipitation, increasing wind speeds, and different soil properties at higher elevations (e.g., Whittaker 1975, Smith et al. 1990, Nikilov and Zeller 1992, Dahlgren et al. 1997). Figure 15 represents a schematic of generalized relationships between elevation, precipitation, and temperature in the basin. It is likely that the elevation–precipitation gradient has substantial influence on patterns of biological diversity in the basin.

The inclusion of distance to mouth along with precipitation and elevation in the first physical PCA factor is an artifact of the morphology of the watersheds in the Lake Tahoe basin. Watersheds on the south and west sides of the basin are generally larger and longer (USGS 1994) than the other 2 orientations because of the greater height of the Sierra Crest compared with the Carson Range. Coincident with this is the higher precipitation on the west and south sides of the basin. The result is the unexpected relationship observed here where distance from the mouth of the stream is more highly correlated with elevation and precipitation that it is with channel characteristics. Typically, streams and rivers exhibit a downstream decrease in gradient along their length. Slopes are steep in the headwaters, and become less so as one proceeds downstream, resulting in a concave longitudinal profile (Allan 1995). Almost everything about a river varies with position along its length, including discharge, width, depth, and velocity. This phenomenon is best reflected in the second PCA factor discussed in the channel characteristics section below.

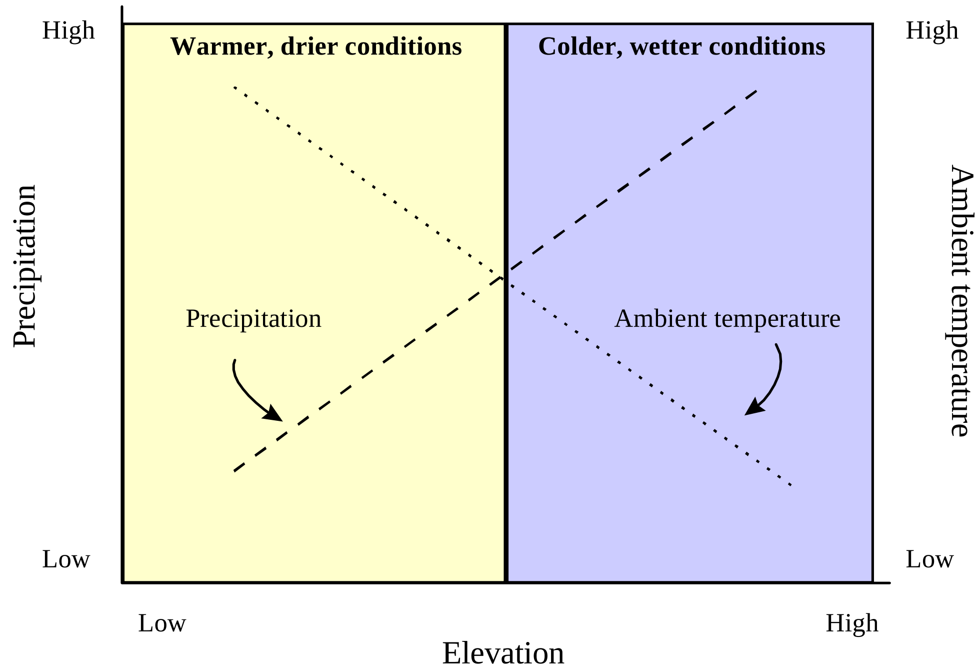

FIG. 15. Generalized relationships between elevation, precipitation, and associated ambient temperature in the Lake Tahoe basin.

Channel Characteristics

Range of Conditions

The three variables describing channel characteristics ranged widely among sample reaches. Gradient is a dominant variable in commonly used classifications for stream channel types (e.g., Rosgen 1994), indicating a useful and meaningful range of conditions in which to study relationships between channel conditions within a stream reach and biological diversity. I used the Rosgen (1994) channel classification scheme (Table 37) as a context for assessing the breadth of channel conditions represented by the sample reaches. Observed stream gradients easily spanned the 0 to 4% range of gradients (slope) used to define Rosgen channel types (Rosgen 1994). Sinuosity values typically range from near 1.0 in simple, well-defined channels to 4.0 in highly meandering channels (Gordon et al. 1992). In this study, sinuosity ranged from 0 to 2.4, readily encompassing the 1.2 to 1.4 that Rosgen (1994) used as a cut-off to differentiate channel types. In contrast to gradient and sinuosity, width is not used directly in the identification channel types by Rosgen. However, the range of stream widths in the basin can serve as an alternate benchmark. Stream widths ranged from less than a meter to 19 m. The largest stream in the basin is the Upper Truckee River, which serves as the primary inlet for Lake Tahoe. Upper Truckee was randomly selected as one of the watersheds, and the lowest reach was located less than 700 m from its mouth. Therefore, sample reaches spanned the range of stream widths in the basin.

TABLE 37. Channel type definitions based on Rosgen's (1994) classification.

Channel type	Slope (%)	Sinuosity	Width/Depth Ratio	Entrenchment
A	> 4	< 1.2	< 12	< 1.4
B	2-4	> 1.2	> 12	1.4-2.2
C	0.1-2.0	> 1.4	> 12	> 2.2
D	0.1-2.0	< 1.2	> 40	multiple channels
E	< 4	> 1.5	< 12	< 2.2
F	< 2	> 1.2	> 12	< 1.4
G	< 2	> 1.2	< 12	< 1.4

Channel Flow Gradient

The differentiation of channel characteristics from other physical features in the PCA provides a strong basis for treating channel characteristics as an entity distinct from other physical features of the landscape. The channel flow gradient serves as a direct measure of channel and flow characteristics, as well as an indirect measure of productivity and biological characteristics. In terms of physical characteristics, the most striking physical changes are steepness of slope and transition from a cooler, shallower stream with rocky substrates to a warmer, deeper stream typically dominated by finer substrates such as sand and silt. A host of biological variables correlate with stream size and transitions from headwaters to mouth (Vannote et al. 1980). The river continuum concept (RCC) (Vannote et al. 1980), describes the change in nutrient dynamics and relative abundance of invertebrates functional groups along a river from headwaters to mouth. The RCC contends that from headwaters to mouth, a stream generally shifts from a system where most of the nutrients are derived from external sources (allochthonous) and the invertebrate community is dominated by shredders and collectors, to a system where a greater proportion of nutrients are generated within the channel (autochthonous) through photosynthesis and the accumulation of nutrients from upstream, and the invertebrate community is dominated more by grazers and collectors. Although the RCC has met only limited success when applied to a variety of types of rivers (Statzner and Higler 1985), an increase in nutrient content and productivity from headwaters to mouth is generally true for all types of rivers (Allan 1995). The channel flow gradient is interpreted as directly representing shifts in geomorphology (including increased channel-floodplain interactions), and indirectly representing increases in productivity.

Vegetation Characteristics

Vegetation Gradients

The vegetation types identified for the purposes of this study were quite broad and pertained to major shifts in dominant plant species. The successful identification of 2 major and 2 minor vegetation gradients based on these data indicate that the resolution of the vegetation data were adequate and appropriate for the purposes of this study. The first major vegetation gradient reflected variation in the dominance of riparian associated vegetation adjacent to the stream. It indicates that the study spanned a wide range of riparian conditions. The strong positive relationship between this gradient and the channel flow gradient further indicates that vegetation factor 1 (forest to meadow) represents the major gradient of vegetative riparian conditions. The second major vegetation gradient reflects the influence of elevation and moisture on woody vegetation types, as defined by the associated vegetation types and reinforced by the strong positive relationship with the elevation–precipitation gradient.

The alder–willow gradient appeared to be independent of any of the environmental variables assessed in this study. The only relationship observed was a negative relationship with mixed conifer. Alder–willow tends to occur in greatest abundance in areas with gentle slopes, open canopy, and channels that are well connected to an adjacent floodplain such that soil moisture is high and inundation is frequent (Allan 1995). The measurement of these variables was beyond the scope of this project, however my results do substantiate that moisture and floodplain connectivity features are likely to be important explanatory variables in studies focused on alder–willow communities in riparian environments.

The aspen–cottonwood gradient was the weakest of the vegetation gradients, but it still explained almost 15% of the variation in vegetation community composition among sample reaches. The negative correlation between aspen–cottonwood and subalpine conifer, as well as the positive relationship between the aspen–cottonwood gradient and the channel flow gradient suggests that low gradient reaches at low to mid elevation sites provide the best environmental conditions for aspen–cottonwood.

Vegetation Types

Mixed Conifer

Mixed conifer was the most frequently occurring forest type. On sample reaches, mixed conifer was not recorded above 2400 m, which is consistent with its general range of occurrence between 1800 and 2500 m in elevation (Whitney 1979). Mixed conifer forests are typically multi-layered with a variety of codominant tree species including white fir, sugar pine, Jeffrey pine, red fir, and lodgepole pine (Barbour and Major 1988, Fites 1993, Holland and Keil 1995, Sawyer and Keeler-Wolf 1995, Franklin and Fites-Kaufmann 1996). Late-seral forests typically have a dense conifer overstory and a sparse understory, and span a number of plant-associations within the mixed conifer series (Fites 1993).

Lodgepole pine

Lodgepole pine was the second most common forest type in the study area, occurring on about 30% of the reaches. Lodgepole pine forests typically occur from 1800 to 2500 m in elevation. Lodgepole pine is commonly the dominant conifer of glacially scoured ridges, valleys, and basins in the lower subalpine zone (Whitney 1979). Lodgepole pine was observed as high as 2541 m (8385 ft) in elevation on sample reaches, conforming to its typical elevational range. It tends to form extensive, open forest of scattered, often pure stands intermingled with lakes, meadows, and granite outcrops (Whitney 1979, Sawyer and Keeler-Wolf 1995). It is also associated with soils that are seasonally flooded and saturated, frequently in moist areas along streams and meadow borders, as observed in the study area. Mature trees are 15 to 25 m tall and 15 to 50 cm dbh. Understory vegetation is sparse in lodgepole pine forests, but frequently consists of a variety of grasses, sagebrush, and forbs (Potter 1994). Therefore, lodgepole pine stands tend to have open, park-like understories with little vertical diversity. As meadows dry out over many years, fire may prevent lodgepole pine from invading meadows, since mature lodgepole pine trees are often killed by fire (Whitney 1979). In the basin where fire has been suppressed for many decades (Weatherspoon et al. 1992, McKelvey et al. 1996, Manley et al. 2000), it is likely that lodgepole pine has become more prevalent throughout the basin, particularly in association with riparian and meadow environments because of the lack of fire.

Subalpine Conifer

Subalpine conifer forests were the third most frequent forest type on sample reaches, occurring on 30% of all reaches. Subalpine conifer forests generally form open woodlands of small groves and scattered individual trees from 2100 to 3400 m (Verner and Purcell 1988), spanning the range of elevations represented by the sample reaches. Subalpine conifer forests of the Lake Tahoe basin appear to be characteristic of subalpine forests throughout the Sierra Nevada, being comprised of red fir, western white pine, and lodgepole pine, and mountain hemlock (Whitney 1979, Barbour and Major 1988, Potter 1994, Sawyer and Keeler-Wolf 1995). Deciduous trees, aside from aspen, are typically absent from the subalpine forest, as are understory herbs and shrubs. Mature pure red fir forests often contain no other conifer because red firs form such dense canopy on favored sites that competitors are shaded out (Oosting and Billings 1943, Potter 1994). Along its lower elevational limit, subalpine conifer forests merge with the lodgepole pine and mixed conifer forests, as reflected in vegetation relationships along vegetation factor 2, while its upper limit constitutes timberline, above which lies the treeless alpine zone. Subalpine conifers commonly occupy sites characterized by moderate to high snow depths and moisture, ranging up to 5 m snow depths during the winter (Barrett 1988).

Riparian Woodlands

Alder–willow and aspen–cottonwood comprised the riparian woodland vegetation types detected in the basin. Each of these 2 vegetation types had different distributions within the basin. The occurrence of alder–willow on over 95% of all reaches indicates that riparian woodland vegetation was prevalent along streams in the basin, and the fact that it rarely dominated reaches (averaging 19.5% cover) indicates a high diversity of plant species composition and structure on most sample reaches (Grenfell 1988). Alder–willow vegetation was most abundant on the north and west sides of the basin. It was in greater abundance in association with mixed conifer than with any other vegetation type.

Aspen–cottonwood was rare on sample reaches, occurring on 16% of the reaches, and when it occurred it never dominated the reach (averaging 2.5% cover). Aspen is typically found near meadow streams and moist flats above 1800 m and can occur as high as 3050 m (DeByle 1985), but it only occurred once above 2300 m in the study area. In the Sierra Nevada, aspen and cottonwood frequently occur together (Parker and Matyas 1981, Sawyer and Keeler-Wolf 1995), although older, undisturbed aspen stands are often monotypic (Verner 1988, Potter 1994). Aspen–cottonwood is associated with soils that are seasonally flooded and permanently saturated, and so are commonly associated with riparian environments (Sawyer and Keeler-Wolf 1995). Aspen stands typically have an open canopied structure and a well developed understory including a high diversity of shrubs, grasses, and particularly herbs (DeByle and Zasada 1980, Mueggler 1985, 1988, Potter 1994, Sawyer and Keeler-Wolf 1995).

Aspen stands are typically ephemeral, being replaced by coniferous trees (or infrequently grasslands and shrublands) if succession progresses without disturbance (Mueggler 1985), however many “stable” aspen stands have been described in the Rocky Mountains (e.g., Lynch 1955, Youngblood and Mueggler 1981, Mueggler and Campbell 1982). Barry (1971) considered most aspen stands in the Sierra Nevada to be stable communities adapted to ecotonal areas between forest and meadows. A known exception to this is in some red fir forests, where aspen can appear as an early seral species (Barry 1971). If conifers are prominent within aspen stands, then it is likely that aspen is not the dominant tree species at climax. Fire is the most common form of disturbance that retains the presence of “seral” aspen stands (Jones and DeByle 1995). It is not known if fire suppression in the basin has affected the extent and character of aspen stands, however grazing is known to alter their vegetative character (Sawyer and Keeler-Wolf 1995).

Shrubs

Shrubs in the study area were grouped into one vegetation class that corresponds closely to the broad vegetation type of montane chaparral (Whitney 1979, Risser and Fry 1988). Montane chaparral typically occurs between 1000 and 3000 m in elevation, spanning the range of elevations in the study area. Montane chaparral typically consists of shrub species adapted to the colder temperatures, deeper snows, shorter growing seasons, and other conditions characteristic of higher elevations (Risser and Fry 1988). It commonly occurs as patches within various forest types, and as large expanses on dry, rocky slopes. Montane chaparral typically forms dense thickets less than 2 m tall, being more compact and lower to the ground than shrub communities at lower elevations. Montane chaparral in the study area, as throughout the Sierra Nevada, typically consisted of huckleberry oak, golden chinquapin, mountain whitethorn (*C. cordulatus*), and pine mat manzanita (*Ceanothus prostratus*). Additional associates included greenleaf manzanita, toboacco brush (*C. velutinus*), California mountain mahogany (*C. betuloides*), snow bush, bitter cherry, and snow berry, with understory herbs commonly being absent.

Montane Meadows

Meadow was present on almost 50% of the sample reaches and dominated some, indicating a substantial influence on the composition and structure of riparian conditions on sample reaches. Montane meadows were observed across the full range of elevations (1800 to 2700 m) in the Lake Tahoe basin, and they ranged in size from small inclusions in forested habitats to large open flats covering several square kilometers. Montane meadows are typically dominated by sedges (*Carex* sp.), but common associates in include perennial herbs, grasses, rushes, and occasional shrubs (Whitney 1979, Ratliff 1988, Sawyer and Keeler-Wolf 1995). They occur in areas that vary from seasonally saturated to semi-permanently flooded. Their association with lodgepole pine in the study area indicates that these 2 vegetation types often form ecotones which are likely to further enhance the diversity of areas with meadow.

Vegetation Type Summary

Riparian vegetation, including alder–willow, aspen–cottonwood, and meadows, provide particularly abundant resources for biota. The uniqueness of their soil and vegetation complexes produce diverse vegetation structure and concomitant diverse biological communities. Many biota are disproportionately more diverse in riparian areas compared to other environments (e.g., Thomas et al. 1979). The interspersion of conifer, shrub, and riparian vegetation on the sample reaches increases the species diversity and structural heterogeneity of the riparian environment, although it may have lower productivity than riparian environments comprised entirely of riparian vegetation. The interplay of productivity and heterogeneity are likely to result in complex relationships between biological diversity and vegetative conditions.

Woody Debris

Snags and logs were prevalent, occurring on all but 2 reaches. The principal components analysis lumped all the snags and terrestrial logs into one gradient that explained over half of the variation in woody debris. The abundance of snags and logs is attributed to a combination of fire suppression and drought, which in turn has led to tree mortality due to drought stress and beetle infestations (Weatherspoon et al. 1992, McKelvey et al. 1996).

Basin Orientation

Many physical gradients, and associated biotic characteristics, varied by orientation to Lake Tahoe. The Lake Tahoe basin is located in a transition zone between the climate and vegetation of the west slope of the Sierra and the Great Basin. For example, the majority of precipitation reaching the basin comes from the west, creating higher average precipitation on the west and south sides of the basin. In addition, the steep slopes of the basin probably influence the amount of solar radiation that each basin orientation receives. As such, the west and east sides of the basin differ substantially in their physical and biological character. The north and south sides of the basin are largely areas of transition between west and east, as well as having unique characteristics of their own related to variations in geology and geomorphology. Such strong gradients of variation among orientations are likely to influence the distribution of biota, potentially having a more pronounced influence on less mobile species because of the barriers that the environmental conditions of some orientations present.